

THE CRETACEOUS SPECIES OF *PYRIPORA* D'ORBIGNY AND *RHAMMATOPORA* LANG

by H. DIGHTON THOMAS and G. P. LARWOOD

ABSTRACT. The Cretaceous species of *Pyripora* d'Orbigny and *Rhammatopora* Lang are revised, and *Rhammatopora gasteri* sp.nov. is described.

IN a recent publication (Thomas and Larwood 1956) we have discussed the status of the genera *Pyripora* d'Orbigny and *Rhammatopora* Lang. We have now investigated in greater detail the Cretaceous species of these genera, in the course of which we have examined several hundred zoaria of species of *Pyripora*. This examination has shown, *inter alia*, that *P. [Herpetopora] anglica* Lang is distinct from *P. [H.] clavigera* Lang, a junior synonym of *P. laxata* (d'Orbigny), and that the two species may be differentiated on the ratio of the length and width of the aperture.

Most of the zoaria of *Pyripora* which we have examined encrust comparatively smooth substrates. Commonly these are fragments of *Inoceramus* shell (40%), pieces of echinoid test (40%), or fragments of *Ostrea* valve (10%). Less frequently zoaria are also found encrusting belemnite guards (5%) and occasionally the remains of other organisms (5%), e.g. brachiopod shell fragments, corals, crinoid plates, and other polyzoa (percentages approximate).

We wish to thank Mr. A. G. Brighton and Mr. R. R. Clarke for the loan of material from the Sedgwick Museum, Cambridge, and the Norwich Castle Museum, respectively; Prof. E. Voigt, of the Geologisches Staatsinstitut, Hamburg, for the loan of German specimens, for information readily given, and for permission to reproduce his photograph of the type specimen of *Hippothoa laxata* d'Orbigny; and Dr. Anna B. Hastings, of the Zoological Department, British Museum (Nat. Hist.), for discussions on the Recent species of *Pyripora*. Except where otherwise stated, the photographs are by Messrs. M. G. Sawyers and J. V. Brown of the British Museum (Nat. Hist.).

The specimens are referred to by their registered numbers in the various museums: those prefixed by the letter D (e.g. D. 2062) are in the British Museum (Nat. Hist.).

PYRIPORA d'Orbigny

Diagnosis. Zoarium encrusting, uni- or pluri-serial; zooecia pyriform, budded distally and uni- or bi-laterally or both, proximally tapered, often with a very slender tubular proximal cauda; aperture longitudinally oval; cryptocyst usually present forming a proximal shelf or a narrow shelf round most of the opesia; gymnocyst well developed proximally; no calcified basal wall; no ovicells, spines, or avicularia.

Remarks. In all the specimens of the Recent species *Pyripora catenularia* (Fleming), and in all the hundreds of zoaria, and therefore thousands of zooecia of *P. laxata* which we have examined, no ovicells were seen. Hence it is certain that ovicells are not developed in the genus. We therefore exclude from *Pyripora* those species which resemble that genus in other characters but possess ovicells.

We have found that, although the size of zooecia may vary considerably in a given

zoarium of a species of *Pyripora*, the ratio of the length and width of the aperture varies essentially within narrow limits, and this ratio, in conjunction with the lengths of the zooecia (excluding the caudae), is of great value in recognizing the species.

We reject certain species from *Pyripora* (see p. 381) and include only those given in the following key.

Key to the Cretaceous species of *Pyripora*

1. Majority of caudae narrow and longer than the rest of the zooecia.
 - (A) Lc commonly well over 1.00 mm.
 - (a) ha = 0.25 to 0.43 mm., la = 0.14 to 0.25 mm., apertural ratio 1.40 to 2.35 *P. laxata* (d'Orbigny)
 - (b) ha = 0.44 to 0.69 mm., la = 0.17 to 0.27 mm., apertural ratio 2.22 to 3.29 *P. anglica* (Lang)
 - (B) Lc = 0.16 to 0.52 mm., ha = 0.10 to 0.15 mm., la = 0.06 to 0.07 mm. *P. filum* (Voigt)
2. Majority of caudae broad and shorter than the rest of the zooecia.
 - (A) Zoarial budding uni- and bi-lateral occasionally becoming pluriserial; caudae nearly as long as the rest of the zooecia *P. texana* Thomas and Larwood
 - (B) Zoarial budding uni- or bi-lateral never becoming pluriserial; caudae distinctly shorter than the rest of the zooecia.
 - (a) Zoarial budding unilateral; zooecia markedly rounded distally; Lz = 1.20 to 1.50 mm., lz = 0.50 mm.; ha = 0.40 mm.; caudae short, very narrow proximally *P. faxensis* (Voigt)
 - (b) Zoarial budding uni- and probably bi-lateral; zooecia more pointed distally; Lz = 0.50 to 0.75 mm., lz = 0.35 to 0.50 mm.; ha = 0.40 to 0.70 mm.; caudae very short and broad *P. parvicauda* (Voigt)
3. Caudae absent. Zooecia very small, Lz = 0.30 to 0.35 mm., lz = 0.25 to 0.30 mm.; gymnocyst very narrow *P. filimargo* (Voigt)

Pyripora laxata (d'Orbigny)

Plate 60, figs. 1, 2; Plate 61, fig. 2

Hippothoa laxata d'Orbigny 1852, pl. 711, figs. 12–15; 1853, p. 386.

Hippothoa cruciata Reuss 1854, p. 134, pl. 28, fig. 1.

non Hippothoa desiderata Novák 1877, p. 86, pl. 2, figs. 1, 2.

Hippothoa labiata Novák 1877, p. 86, pl. 3, figs. 1–5.

Herpetopora clavigera Lang 1914a, p. 6, pl. 2, figs. 4, 5; Voigt 1930, pp. 409, 553, pl. 1, figs. 2, 3; 1949, p. 10, pl. 1, figs. 4–6.

Herpetopora cruciata (Reuss); Lang 1914a, pp. 6, 7.

Herpetopora dispersa (von Hagenow); Voigt 1930, pp. 409, 553, pl. 1, fig. 1; [*non Cellepora dispersa* von Hagenow 1839, p. 280; 1846, p. 629, pl. 23b, fig. 55].

Herpetopora comptouieusis Brydone 1936, p. 88, pl. 42, fig. 17.

Pyripora cruciata (Reuss); Thomas and Larwood 1956, p. 375 [*partim*].

Lectotype (here chosen). Specimen encrusting an *Echinocorys* test. Senonian, zone of *Belemnitella mucronata*, Meudon, south-west of Paris. D'Orbigny Collection No. 7911, Muséum National d'Histoire naturelle, Paris.

Diagnosis. *Pyripora* in which the lateral budding is usually bilateral but sometimes unilateral; zooecia inflated, 0.24 to 0.45 mm. wide, with steep lateral walls, distally rounded or slightly tapering, proximally tapered; calcification of frontal membrane

and of operculum, and regeneration, relatively common; aperture longitudinally oval, $h_a = 0.25$ to 0.43 mm., $l_a = 0.14$ to 0.25 mm., apertural ratio = 1.40 to 2.35 but mostly 1.7 to 1.9 ; cryptocyst a narrow shelf extending about three-quarters of the way round the opesia; caudae very narrow, tubular, varying greatly in length but usually much longer than the rest of the zooecia, expanding rapidly into the triangular proximal gymnocyst of the zooecium; triangular kenozooecia, with a rounded pore, occasionally occur.

Description. Zoarium encrusting, with distal-median, and usually bilateral, but sometimes unilateral, budding. The distal-median budding is usually single, but very occasionally it may be double. Bilateral budding is more common than unilateral, though both occur at times in the same zoarium. This budding is usually from the distal-lateral walls of zooecia and may be at right angles to them or directed distally and obliquely at a lesser angle. In any one series of zooecia unilateral budding may occur on either side. Sometimes the budding, whether uni- or bi-lateral, may develop from the caudae.

Caudae slender, tubular and of very variable length—in rare instances absent or very short. The caudae may, however, be several times the length of the rest of the zooecia. In any series of zooecia successive caudae are commonly increasingly longer. They are generally straight but may be variously curved. They rapidly expand into the triangular, proximal, smooth gymnocyst of the zooecia: the length of the gymnocyst varies, but it is generally well developed.

Zooecia pyriform, longitudinally oval, inflated; lateral and distal walls steep, the latter rounded or slightly pointed distally; calcified basal walls absent in the fossil state. Aperture longitudinally oval, of smaller size but relatively wider than in *Pyripora anglica* (Lang) (cf. text-figs. 1b–d). The apertural ratio = 1.40 to 2.35 but is mostly 1.7 to

EXPLANATION OF PLATE 60

Figs. 1, 2. *Pyripora laxata* (d'Orbigny). 1, Type specimen, Mus. nat. Hist. nat. Paris, d'Orbigny Collection No. 7911, encrusting test of *Echinocorys*, normal zooecia with, at left, one zooecium with calcified frontal membrane with central pore, $\times 20$. Photograph by Prof. E. Voigt. 2, Part of the holotype of *Herpetopora clavigera* Lang, Brit. Mus. (Nat. Hist.) 40246, several series of uni- and bi-laterally budded zooecia which have overgrown each other; one zooecium has a calcified frontal membrane and operculum, $\times 20$.

FIGS. 3, 4. *Pyripora anglica* (Lang). 3, Paratype, D. 10074, uni- and bi-laterally budded zooecia, one with a calcified frontal membrane and operculum, and one heterozooecium, $\times 20$. 4, Holotype, D. 11359, uni- and bi-laterally budded zooecia, some with the frontal membrane and operculum calcified and some regenerated. The linear series of partly developed zooecia is typical of some zoaria, $\times 20$.

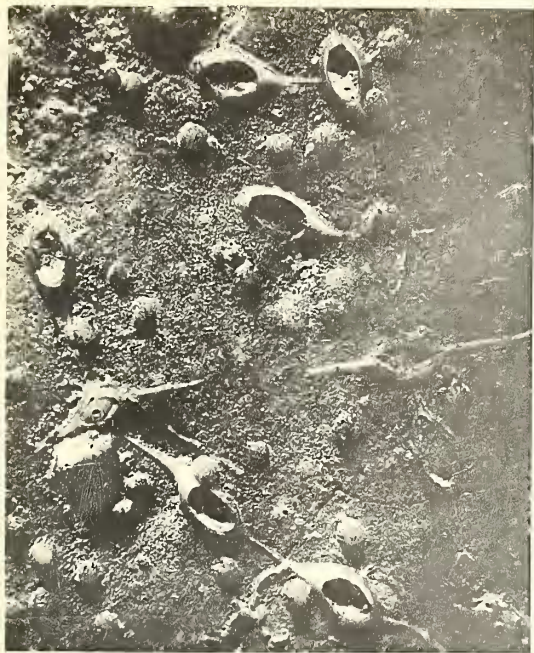
EXPLANATION OF PLATE 61

Fig. 1. *Pyripora anglica* (Lang), paratype, D. 21957. Part of a uni- and bi-laterally budded zoarium showing the tendency for successive zooecia to develop increasingly longer caudae, the occurrence of calcified zooecia in linear series and a triangular heterozooecium, $\times 20$.

Fig. 2. *Pyripora laxata* (d'Orbigny). Holotype of *Herpetopora comptoniensis* Brydone, Sedgwick Museum, B. 36997. Normal zooecia, one with a calcified frontal membrane, $\times 20$.

Figs. 3, 4. *Pyripora filum* (Voigt), Voigt Collection No. 1532. 3, Normal zooecia with thread-like caudae and strongly inflated distal portions encrusting branches of a cyclostomatous polyzoan, $\times 35$. 4, Two smaller normal zooecia of the same specimen with shorter caudae, $\times 35$. Photographs by Department of Photography, University of Durham, King's College, Newcastle upon Tyne.

Fig. 5. *Pyripora texana* Thomas and Larwood, holotype, D. 40541. Uniserially budded normal zooecia in part of the zoarium, $\times 20$.







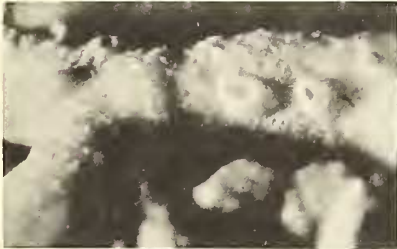
1



2



3



4



5



1-9. Cryptocyst narrow, slightly descending, extending most of the way round the aperture and producing an oval opesia only slightly smaller than the aperture. Calcification of the frontal membrane and of the operculum is common. It is often complete, but at times incomplete, leaving a small, circular, uncalcified portion near the middle, showing that the calcification has spread from the margin inwards. The calcified opercula are small, straight sided, and evenly rounded distally. Lateral budding frequently, but not always, takes place from zooecia which are thus calcified. Regeneration of zooecia is fairly common and may occur more than once in a given zoecium (text-fig. 1e). Sometimes regenerated zooecia have the frontal membrane and operculum completely calcified (text-fig. 1f-g).

Kenozoecia are fairly common, and are inflated, triangular, and apparently vicarious: they usually have a rounded, median pore and often bud to give normal zooecia.

Avicularia, spines, and ovicells absent.

Measurements (see text-fig. 1a)

Zooecia	Lz = 0.66 to 5.18 mm. (or more).	ho = 0.23 to 0.41 mm.
	lz = 0.24 to 0.45 mm.	lo = 0.13 to 0.14 mm.
	ha = 0.25 to 0.43 mm.	Lc = up to 4.00 mm. (or more).
	la = 0.14 to 0.25 mm.	lc = about 0.07 mm. (unless absent).

Apertural ratio = 1.40 to 2.35, but mostly 1.7 to 1.9.

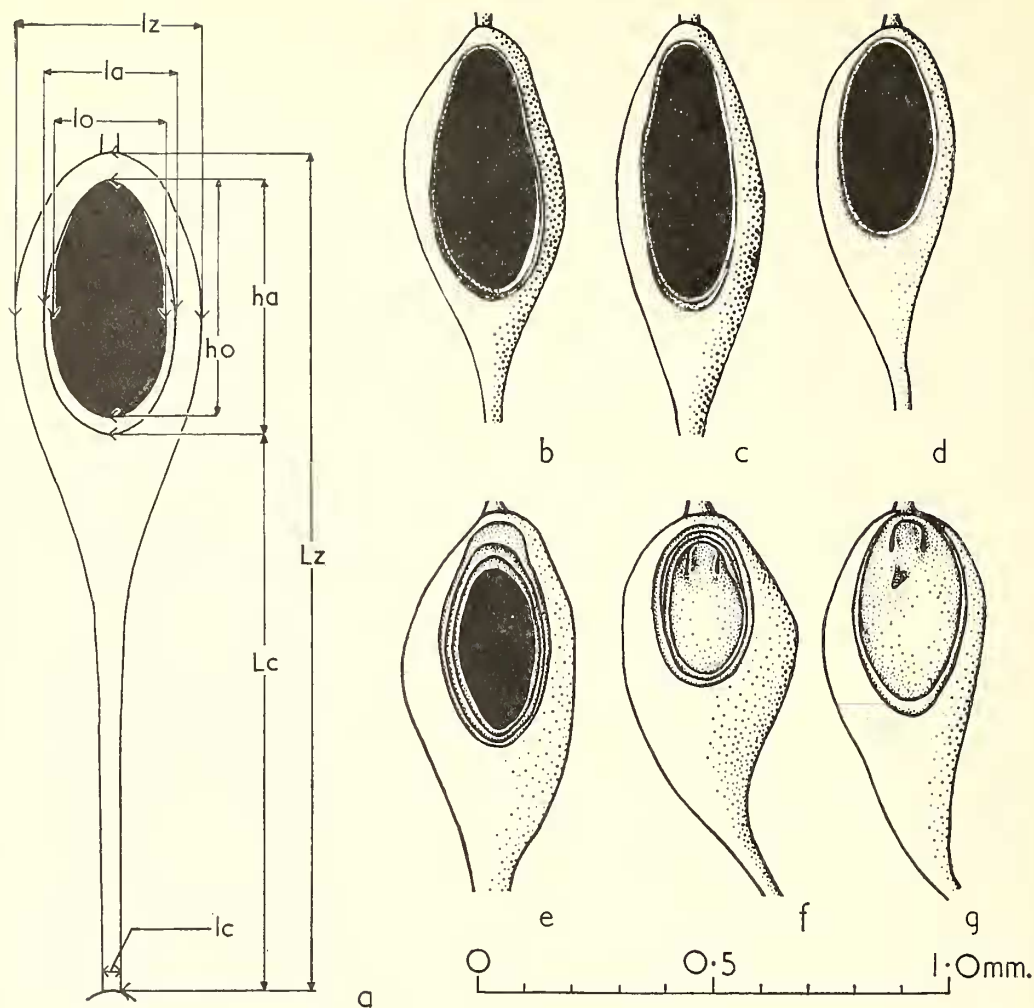
Measurements of a large number of zooecia have been made on specimens ranging from the Cenomanian to the Danian. Lz is widely variable, for it includes measurement of the cauda as well as the rest of the zoecium; lz, ha, la, ho, and lo are less variable than Lz or the caudal measurements (Lc, lc), and are consequently of greater diagnostic value. Lc is extremely variable; caudae may be lacking, or they may be up to three or four or more times as long as the rest of the zooecia; the caudae are, however, always very narrow.

Remarks. This revision shows that wide variation may occur not only between zoaria but also within the zoaria themselves.

In 1839 von Hagenow briefly described (p. 280) a polyzoan from Rügen as *Cellepora dispersa*: unfortunately he gave no figure. Subsequently (1846, p. 629, pl. 23b, fig. 55), he gave a more detailed description of the species, accompanied by a figure, on which the interpretation of *Cellepora dispersa* must be based. In the upper right-hand part of the figure he showed three circular heterozooecia which can be matched in a species from Rügen which Lang (1914b, p. 439, pl. 34, fig. 3) described as *Marssonopora dispersa* (von Hagenow). We agree with Lang's interpretation. Thus, in contrast to Voigt's opinion (1930, p. 409) von Hagenow's specific name *dispersa* is not available for the Chalk species lacking avicularia.

Lang (1914a, p. 7) considered *Hippothoa gracilis* d'Orbigny (1852, pl. 711, figs. 12-15; 1853, p. 386) to be a species of his genus *Herpetopora*, but the nature of its orifice and the occurrence of ovicells show clearly that it does not belong to that genus, and, therefore, not to *Pyripora*.

Prof. E. Voigt has recently sent us photographs of the type specimen of *Hippothoa laxata* d'Orbigny (1852, pl. 711, figs. 12-15; 1853, p. 386), d'Orbigny Collection No. 7911. From these it is clear that the species is the same as *Herpetopora clavigera* Lang of which



TEXT-FIG. 1. *a*, Measurements: Lz = length of zooecium; lz = width of zooecium; ha = length of aperture; la = width of aperture; ho = length of opesia; lo = width of opesia; Lc = length of cauda; lc = width of cauda. *b, c*, Distal ends of two normal zooecia of *Pyripora anglica* (Lang): (*b* and *c* from D. 40489). *d-g*, Distal ends of zooecia of *P. laxata* (d'Orbigny): (*d*—D. 40135, normal zooecium; *e*—D. 40158, repeatedly regenerated; *f*—D. 40364, repeatedly regenerated with completely calcified frontal membrane and operculum; *g*—D. 40140, regenerated with completely calcified frontal membrane and operculum).

we have much well-preserved material. *Hippothoa laxata* d'Orbigny therefore becomes the first available name for the species dealt with here.

Hippothoa desiderata Novák (1877, p. 10, pl. 2, figs. 1, 2) was placed by Lang (1914*a*, p. 7) in *Herpetopora*, but *Hippothoa desiderata* was described by Novák as possessing small, hemispherical ovicells. The species is thus excluded from *Pyripora*.

Among the large number of specimens from the English, and some foreign, Chalk which we have examined there are variations in the branching and in the caudal and

other zoecial characters which show that *Hippothoa laxata* d'Orbigny (1852; 1853), *H. cruciata* Reuss (1854), *H. labiata* Novák (1877), *H. dispersa* Marsson (1877) *non* von Hagenow, *Herpetopora clavigera* Lang (1914a) and *H. comptouiensis* Brydone (1936) are all synonymous.

The species is widely distributed in Europe—see the localities to which the references in the synonymy apply. Prof. E. Voigt has recently sent us a photograph of a specimen encrusting a *Gryphaea* from the Maastrichtian of Burunduk Kaja, Crimea (Coll. Inst. Hist. Geol. Fac. Geol. Moscow, No. 8084-5/b), which he had received from Prof. Najdin of Moscow. He has also told us of a specimen he had found on an *Echinocorys* from the Upper Maastrichtian of Hallembaye, near Haccourt, north-east of Liège, Belgium.

Stratigraphical distribution. Cenomanian, zone of *Schloenbachia varians*, to Danian (see remarks on *Pyripora anglica*).

Specimens. A. British. From numerous localities in south-east and east England, ranging from Dorset and the Isle of Wight to Lincolnshire. (1) British Museum (Natural History): (a) Zone of *Belemniteella mucronata*—43 specimens including 40246, D. 3243, D. 20607-8, D. 28898, D. 40135, and D. 40140. (b) Zone of *Gonioteuthis* [*Actinocamax*] *quadrata*—169 specimens including D. 2647, D. 3244, D. 20610, D. 28081-100, D. 28795, D. 29054, D. 29063, D. 40158, and D. 40364. (c) Zone of *Offaster pilula*—D. 28917, D. 29842-5, D. 40532-3. (d) Horizon and locality unknown—D. 35352. (2) Norwich Castle Museum: Zone of *B. mucronata*—N.C.M. 76.937(34-39). (3) Sedgwick Museum: (a) Zone of *Ostrea lunata*—B. 60756-60, B. 61001-2, B. 80750-60. (b) Zone of *B. mucronata*—B. 80676, B. 80691-749. (c) Zone of *G. [A.] quadrata*—B. 80675, B. 80677-88. (d) Zone of *B. mucronata* or *G. [A.] quadrata*—B. 80689-90. (e) Zone of *O. pilula*—B. 80674. (f) Zone of *Schloenbachia varians*—B. 36997, type specimen of *Herpetopora comptoniensis* Brydone.

B. Danish. Danian. Faxø, Seeland—?D. 9113, ?D. 29014, ?D. 40537-8.

C. German specimens lent by Prof. E. Voigt, Geologisches Staatsinstitut, Hamburg. (a) Upper Maastrichtian, Hemmoor, Coll. Voigt 3171, 3173. (b) Lower Maastrichtian, Hemmoor, Coll. Voigt 3166; Luneburg (Zeltburg), Coll. Voigt 3167, 3168; and Rügen, Coll. Voigt 3163-5. (c) Maastrichtian, division unspecified, Hemmoor, Coll. Voigt 3172. (d) Zone of *B. mucronata* or *G. [A.] quadrata*, Grube Alsen, near Lägerdorf, Coll. Voigt 3169. (e) Zone of *G. [A.] quadrata*, Lägerdorf, Coll. Voigt 3170.

Pyripora anglica (Lang)

Plate 60, figs. 3, 4; Plate 61, fig. 1

Herpetopora anglica Lang 1914a, pp. 6, 7, pl. 2, figs. 1-3; 1914b, p. 436; 1921, p. 83; 1925, p. 229, pl. 20, fig. 7, pl. 21, fig. 18; Canu and Bassler 1920, p. 81, text-fig. 22; 1923, p. 18, text-fig. 1c; Bassler 1935, p. 124; 1953, p. G157, text-fig. 119, 8.

Pyripora cruciata (Reuss) Thomas and Larwood 1956, p. 370 [*partim*].

Holotype. D. 11359. Specimen encrusting large fragment of *Volvinoceramus involutus*. Senonian, base of zone of *Micraster coranguinum* or top of zone of *M. cortestudinarium*, Chatham, Kent; W. Gamble Collection.

Diagnosis. *Pyripora* like *P. laxata* (d'Orbigny) but $ha = 0.44$ to 0.69 mm., $la = 0.17$ to 0.27 mm., apertural ratio = 2.22 to 3.29 , but mostly about 2.5 .

Measurements

Zoecia	Lz = 0.69 to 4.89 mm. (or more).	ho = 0.42 to 0.67 mm.
	lz = 0.25 to 0.47 mm.	lo = 0.16 to 0.26 mm.
	ha = 0.44 to 0.69 mm.	lc = 0 to 3.87 mm. (or more).
	la = 0.17 to 0.27 mm.	lc = about 0.08 mm., unless absent.

Apertural ratio = 2.22 to 3.29 (mostly about 2.5).

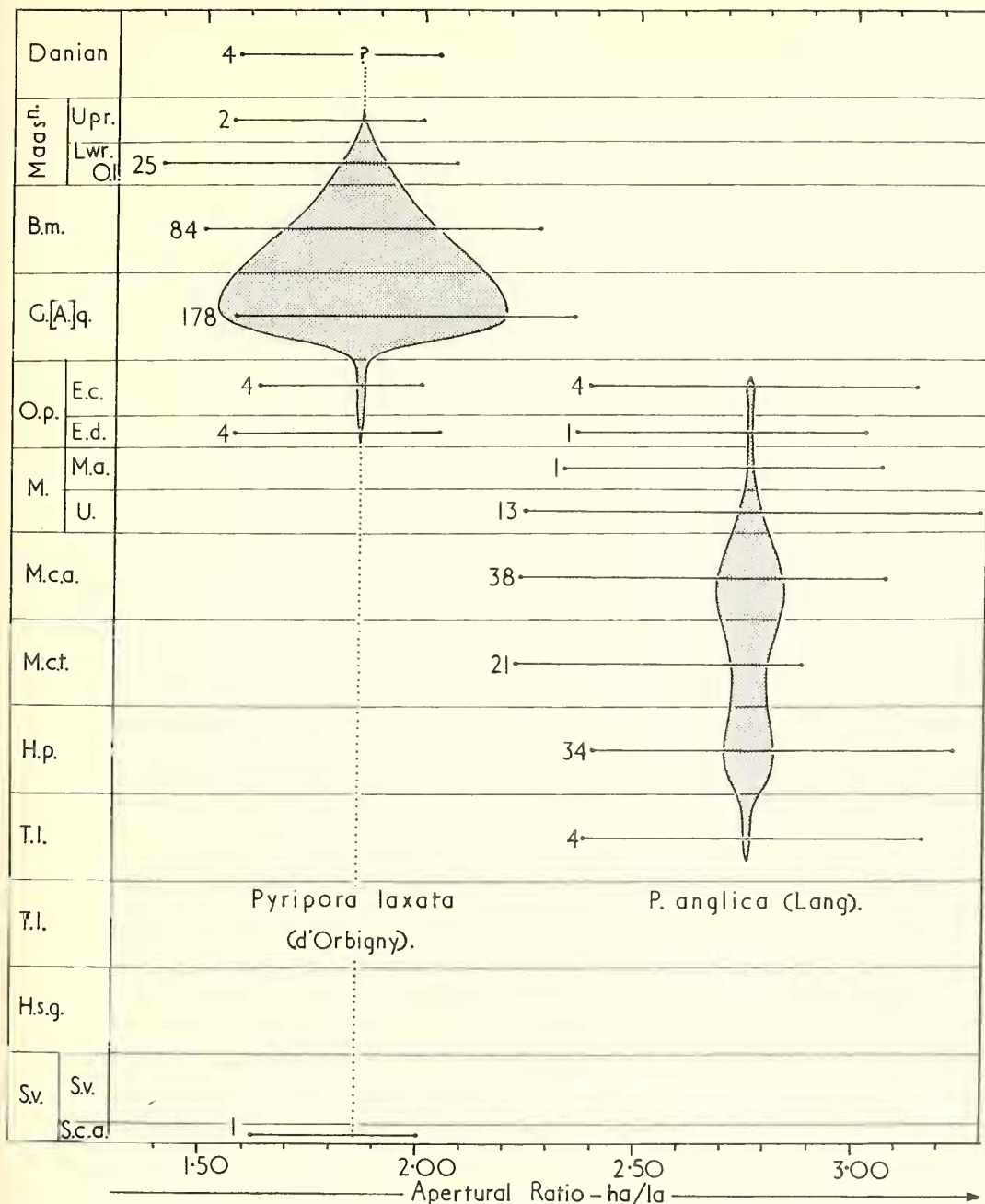
Remarks. *P. anglica* (Lang) very closely resembles *P. laxata* (d'Orbigny) in its zoarial and zooecial characters. The mode of budding of the zoarium is the same; caudae are of the same narrow type though apparently very slightly wider, frequently of increasing length in a given single series; but the zooecia, excluding the caudae, are usually longer. The aperture is larger and distinctly longer and narrower than in *P. laxata* (cf. text-figs. 1b-d), and the gymnocyst proportionately smaller. Other characters, such as the presence of a narrow, proximal cryptocyst, the occurrence of series of sealed zooecia, and the presence of regenerated zooecia and triangular kenozooecia are the same.

Lang (1914a) diagnosed *Herpetopora anglica* as having 'zooecia that taper somewhat distally as well as proximally; with regularly elliptical termens [apertural margins]'. As distinct from this, he defined *H. clavigera* as a '*Herpetopora* with zooecia hardly tapering distally and consequently more or less pear-shaped, having their outlines bounded by steeply curved sides . . .'. These distinctions in the general shape of the zooecia of *H. anglica* and *H. clavigera* are not clear either in the new material which we have examined or in Lang's original specimens. In his key to the genus *Herpetopora* (1914a, p. 7) Lang has described the termen [apertural margin] as 'elliptical rather than oval' in *H. anglica*; in other words the aperture is longer and narrower in this species, the apertural ratio being about 2.5. This and the somewhat larger zooecia are the only significantly constant differences from *H. clavigera* Lang, and are clearly confirmed here by many measurements on abundant material of both species.

P. anglica (Lang) is less common than *P. laxata* (d'Orbigny) and has a more restricted stratigraphical range in the English Chalk. Lang (1913, p. 172) has referred to *Herpetopora clavigera* [= *Pyripora laxata* (d'Orbigny)] and to *Herpetopora anglica* [= *Pyripora anglica* (Lang)] as species which 'divide the English Chalk between them at the junction of the *quadratus* and *Marsupites* zones'. Our examination of these species supports Lang's statement but has shown that *Pyripora laxata* (d'Orbigny) first occurs in the Cenomanian where it is represented by one well-preserved zoarium, Sedgwick Museum, B. 36997 (the type specimen of *Herpetopora comptoniensis* Brydone). The species next occurs in the zone of *Offaster pilula* and becomes very abundant in the succeeding zones, possibly surviving into the Danian from which we have seen four rather poorly preserved specimens. In contrast, *Pyripora anglica* (Lang) first occurs in the zone of *Terebratulina lata* and becomes more abundant in the zones of *Holaster planus*, *Micraster cortestudinarium*, and *M. coranguinum*, and survives, much reduced in numbers, into the upper part of the zone of *Offaster pilula* (see text-fig. 2).

Stratigraphical distribution. Turonian, zone of *Terebratulina lata*, to Senonian, zone of *Offaster pilula*.

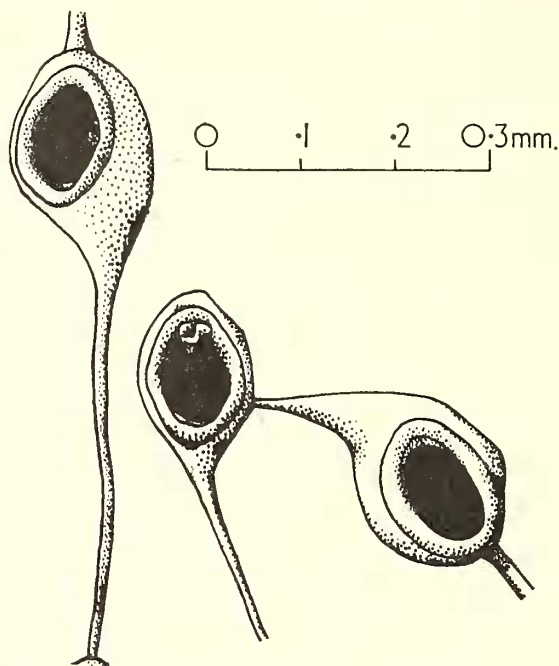
Specimens. From numerous localities in south-east and east England. (1) British Museum (Natural History): (a) Zone of *Offaster pilula*—D. 28239, D. 29846, D. 40529–31. (b) Zone of *Marsupites testudinarium*—D. 29847, D. 40526–8. (c) Zone of *Micraster coranguinum*—D. 4189, D. 8213, D. 10074, D. 11126, D. 21218, D. 21955–8, D. 24361–2, D. 28240–1, D. 28899–900, D. 29098, D. 31825, and 22 other specimens. (d) Zone of *M. cortestudinarium*—D. 8214, D. 11359, D. 21949–51, D. 28242–3, D. 29847, D. 40504–12. (e) Zone of *M. coranguinum* or *M. cortestudinarium*—D. 11372. (f) Zone of *Holaster planus*—D. 8387, D. 21219, D. 29848, D. 40489, and 30 other specimens. (g) Zone of *Terebratulina lata*—D. 20611, D. 40332–4. (h) Horizon and locality unknown—D. 38849. (2) Sedgwick Museum: (a) Zone of *Marsupites testudinarium*—B. 80662–7, B. 80670–3. (b) Zone of *Micraster cortestudinarium*—B. 80655–60.



TEXT-FIG. 2. Stratigraphical distribution of *Pyripora laxata* (d'Orbigny) and *P. anglica* (Lang). The range in value of apertural ratios is shown for 415 specimens from the Chalk. The figures to the left of each line indicate the number of measurable specimens available to us from each zone. (Maasn.—Maastrichtian; O.I.—zone of *Ostrea lunata*; B.m.—zone of *Belemnitella mucronata*; G.[A].q.—zone of *Goniatolithis* [*Actinocamax*] *quadrata*; O.p.—zone of *Offaster pilula*; E.c.—subzone of *Echinocorys scutata* var. *cincta*; E.d.—subzone of *E. scutata* var. *depressula*; M.—zone of *Marsupites testudinarius*; M.a.—subzone of *M. testudinarius*; U.—subzone of *Urtacrinus westfalicus*; M.c.a.—zone of *Micraster coranguinum*; M.ct.—zone of *M. cortestudinarius*; H.p.—zone of *Holaster planus*; T.l.—zone of *Terebratulina lata*; R.c.—zone of *Orbirlhynchia* [*Rhynchonella*] *cuvieri*; H.s.g.—zone of *Holaster subglobosus*; S.v.—zone and subzone of *Schloenbachia varians*; S.c.a.—subzone of *Stauronema carteri*).

Pyripora filum (Voigt)

Plate 61, figs. 3, 4

Herpetopora filum Voigt 1930, pp. 410, 553, pl. 1, figs. 8-10.?non *Herpetopora filum* Voigt; Balavoine 1956, p. 157, pl. 6, fig. 2.*Type specimen.* That figured by Voigt 1930, pl. 1, fig. 10. Maastrichtian. Maastricht.*Diagnosis.* *Pyripora* with small, strongly inflated zooecia; apertural rim thick and prominent; $ha = 0.10$ to 0.15 mm., $la = 0.06$ to 0.07 mm.; small proximal cryptocyst present; $Lc = 0.16$ to 0.52 mm., $lc = 0.02$ to 0.155 mm.

TEXT-FIG. 3. Three normal zooecia of *Pyripora filum* (Voigt).
E. Voigt Collection 1532. Upper Maastrichtian, Maastricht.

Description. Zoarium encrusting, with single distal-median and uni- and bi-lateral budding. Bilateral budding is apparently more common than unilateral, but both may occur in the same zoarium (e.g. Voigt 1930, pl. 1, fig. 9 and Voigt Collection 1532). Lateral budding is commonly from the distal-lateral walls of zooecia and is directed distally and obliquely.

Caudae straight, or only slightly irregular, tubular, very narrow, of variable length with a maximum of 1.00 mm. (see Voigt, 1930, p. 410) but usually much shorter. A cauda may be twice as long as the rest of the zooecium. The caudae expand abruptly into a proximal, triangular, smooth gymnocyst which is nearly as long as the aperture and which rises steeply to the apertural rim and extends, much narrowed, round the aperture.

Zooecia longitudinally oval, strongly inflated; lateral and distal walls fairly steep.

Aperture longitudinally oval, small, with a prominent wide rim. Cryptocyst a slight, crescentic, sloping shelf within the proximal margin of the aperture. Opesium only slightly smaller than the aperture. Calcification of the frontal membrane may be complete (e.g. Voigt, 1930, pl. 1, fig. 9); calcification of the operculum and regeneration of the zooecia have not been seen.

Kenozoecia not seen.

Spines, avicularia, and ovicells absent.

Measurements

Zooecia	Lz = 0.28 to 0.65 mm.	ho = 0.09 mm.
	lz = 0.12 to 0.15 mm.	lo = 0.06 mm.
	ha = 0.10 to 0.15 mm.	Lc = 0.16 to 0.52 mm. (occasionally up to 1.00 mm.).
	la = 0.06 to 0.07 mm.	lc = 0.02 to 0.155 mm.

Apertural ratio = 1.66.

Remarks. *P. filum* (Voigt) is distinguished from other caudate Cretaceous *Pyripora* species by its unusually small size, its prominent, wide apertural rim, and its straight, narrow caudae (see text-fig. 3).

The type specimen from Maastricht is, according to Voigt's description, more robust than the material which he has seen from the *Goniotenthis* [*Actinocamax*] *mammillata* Chalk of Ifö, Sweden. Balavoine (1956, p. 157, pl. 6, fig. 2) has described, as *Herpetopora filum* Voigt, a specimen from limestones containing *Hercoglossa danica* at Vigny, Seine-et-Oise, France. Its very small size (Lz = 0.12 to 0.15 mm., lz = 0.05 to 0.06 mm.) distinguishes it from *P. filum* (Voigt) as described above.

Stratigraphical distribution. Senonian, *G. [A.] mammillata* Chalk (upper part of zone of *G. [A.] quadrata*) and Upper Maastrichtian.

Specimen. Part of a zoarium encrusting a ramose cyclostomatous polyzoan; Upper Maastrichtian, 'Nd Geul-Tal b. Berg b. Maastricht'; E. Voigt Collection 1532.

Pyripora texana Thomas and Larwood

Plate 61, fig. 5

Pyripora texana Thomas and Larwood 1956, pp. 371, 372, text-figs. 2, 3.

Diagnosis. *Pyripora* with somewhat irregular uni- or bi-lateral budding, sometimes becoming pluriserial; Lz = 0.72 to 0.93 mm., lz = 0.21 to 0.33 mm.; ha = 0.33 to 0.36 mm., la = 0.15 to 0.21 mm.; caudae relatively broad, about as long as the rest of the zooecia, Lc = 0.30 to 0.50 mm., lc = 0.07 to 0.10 mm.

Remarks. This earliest known species of *Pyripora* has been described recently by the present authors.

Pyripora faxensis (Voigt)

Herpetopora faxensis Voigt 1930, pp. 410, 553, pl. 1, fig. 4.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 4. Danian. Faxø, Seeland, Denmark.

Diagnosis (based on Voigt's 1930 description and figure). *Pyripora* with zooecia inflated, well rounded distally, tapered proximally, Lz = 1.20 to 1.50 mm., lz = 0.50 mm.;

aperture oval, not much longer than wide, $ha = 0.40$ mm.; proximal cryptocyst apparently present; caudae short, tubular, rapidly widening distally into a long, wide, triangular, proximal gymnocyst.

Measurements (according to Voigt 1930, p. 410)

Zooecia	Lz = 1.20 to 1.50 mm.	ha = 0.40 mm.
	lz = 0.50 mm.	(no other measurements recorded)

Remarks. Voigt (1930, p. 410) has suggested, 'Apparently this [*P. faxensis*] is the largest species of the *dispersa* group—and is thereby distinguished from the other species' [translation]. Voigt's term '*dispersa* group' implies all the Cretaceous species of *Pyripora*, other than *P. texana*, which possess caudae. In addition to the generally greater size of zooecia in *P. faxensis*, their marked distal rounding, the oval aperture, which is almost as wide as long, the short, straight caudae, and the long, wide, triangular, proximal gymnocyst also appear to be of diagnostic value. There are no specimens in the collections examined.

Stratigraphical distribution. Danian.

Pyripora parvicauda (Voigt)

Herpetopora parvicauda Voigt 1930, pp. 411, 553, pl. 1, fig. 11.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 11. 'Oberer Emscher.' Lengede-Broistedt, Gr. Ilse.

Diagnosis (based on Voigt's 1930 description and figure). *Pyripora* with zooecia distally pointed; Lz = 0.50 to 0.75 mm., lz = 0.35 to 0.50 mm.; caudae very short and broad; la = 0.40 to 0.70 mm.; cryptocyst apparently present; gymnocyst narrow distally and laterally, wider and somewhat triangular proximally.

Measurements (according to Voigt 1930, p. 411)

Zooecia	Lz = 0.50 to 0.75 mm.	ha = 0.40 to 0.70 mm.
	lz = 0.35 to 0.50 mm.	(no other measurements recorded).

Remarks. *Pyripora parvicauda* is distinguished particularly by its 'very short caudal part' which is 'hardly developed' (Voigt, 1930, p. 411, translation). The distally pointed zooecial outline is also distinctive. There are no specimens in the collections examined.

Stratigraphical distribution. Senonian, upper part of the Emscherian (? zone of *Micraster coranguinum* or zone of *Marsupites testudinaris*).

Pyripora filimargo (Voigt)

Herpetopora filimargo Voigt 1930, pp. 411, 553, pl. 1, fig. 12.

Type specimen. That figured by Voigt 1930, pl. 1, fig. 12. 'Mammillatensenon' (upper part of zone of *Gonioteuthis* [*Actinocamax*] *quadrata*). Ifö, Sweden.

Diagnosis (based on Voigt's 1930 description and figure). *Pyripora* with zooecia in which Lz = 0.30 to 0.35 mm., lz = 0.25 to 0.30 mm.; caudae absent; cryptocyst apparently absent; gymnocyst very narrow.

Measurements (according to Voigt 1930, p. 411)

Zooecia Lz = 0.30 to 0.35 mm. lz = 0.25 to 0.30 mm.
(no other measurements recorded)

Remarks. The absence of caudae is particularly distinctive in this species, and, as Voigt (1930, p. 411) has stated, the zooecia are very small with an 'exceptionally narrow border [gymnocyst]' (translation). There are no specimens in the collections examined.

Stratigraphical distribution. 'Mammillatensenon' (upper part of zone of *Gonioteuthis* [A]. *quadrata*).

Species previously assigned to *Herpetopora* (= *Pyripora*) but here excluded from *Pyripora*

1. *Herpetopora danica* Lang (1914a, p. 7, pl. 2, figs. 6, 7). Prof. E. Voigt has very kindly lent us a well-preserved specimen, E. Voigt Coll. 3174, from the Upper Maastrichtian of Hemmoor, encrusting a piece of echinoid test. This specimen is like the holotype in its fundamental features, but at least three zooecia have prominent hyperstomial ovicells. It is clear that although ovicells occur they are not frequent and that in less extensive zoaria they may not therefore be present—as is the case in the holotype of *Herpetopora danica* Lang (D. 19429) and in the paratype (D. 44407). However, as all other zoarial and zooecial characters are so similar, the species as a whole may be regarded as ovicelled and therefore excluded from *Pyripora*. We would refer it provisionally to *Membranipora* s.l.

2. *Herpetopora danica* Lang subsp. *titania* Voigt (1949, p. 9, pl. 1, figs. 1–3). We agree that this subspecies, the type of which has been lent to us by Prof. Voigt (E. Voigt Coll., 135), belongs to *Herpetopora danica*. As it belongs to an ovicelled species it also is excluded from *Pyripora*.

RHAMMATOPORA Lang

?*Crisia* Mantell 1844, p. 285; 1854, p. 269.

?*Hippothoa* Morris 1854, p. 125 [*partim*].

Membranipora Vine 1890, p. 484 [*partim*]; 1891a, p. 385 [*partim*]; ? 1891b, p. 395; 1892, p. 154; 1893, p. 335 [*partim*].

Rhammatopora Lang 1915, p. 496 [*partim*—*Crisia johoustoniana* Mantell excl.]; Canu, 1916, p. 58; Thomas and Larwood 1956, p. 372.

Pyripora: Bassler, 1935, pp. 23, 181 [*partim*]; 1953, p. G158 [*partim*].

Type species (by original designation). *Membranipora gaultina* Vine 1890, p. 484, pl. 19, figs. 13a–d, Gault. Cambridge.

Diagnosis. Zoarium encrusting, uniserial; zooecia pyriform, budded distally and uni- or bi-laterally or both, proximally tapered, with slender, tubular, proximal caudae; aperture longitudinally oval; cryptocyst forming a narrow descending shelf, particularly on the proximal side of the opesia; gymnocyst well developed proximally; differs from *Pyripora* in having an apertural rim slightly raised with numerous small apertural spine-bases; no calcified basal wall; no avicularia or ovicells.

Remarks. We have already indicated elsewhere (Thomas and Larwood, 1956, p. 372) that the 'rhamma', described by Lang (1915, p. 497) as a feature of generic importance, is of no systematic significance: it is an irregular crack developed along the caudae

during fossilization. However, *Rhammatopora* Lang may be distinguished from *Pyripora* d'Orbigny by its numerous small apertural spine-bases. We thus differ from Canu (1916, p. 59) and from Bassler (1935, pp. 23, 181; 1953, p. G158) who regarded the two genera as synonymous.

Charixa vennensis Lang, the type species of *Charixa* Lang (1915, p. 500), is a multi-serial species which becomes uni-serial in places (op. cit., pl. 17, fig. 5). In other respects, e.g. the presence of apertural spine-bases, it resembles *Rhammatopora*, and it seems to bear a similar relationship to *R. gaultina* as *Pyripora pyriformis* (Michelin) does to *P. laxata* (d'Orbigny)—see Thomas and Larwood (1956, p. 370). But more material is needed to elucidate further the structure of *Charixa*.

Distelopora Lang (1915, p. 502) differs from *Rhammatopora* in possessing a very wide, distinctive cryptocyst, which contrasts with the slight, narrow, proximal cryptocyst of *Rhammatopora*.

Lang (1915, p. 498) regarded *Crisia johnstoniana* Mantell as a species of *Rhammatopora*. As he pointed out, only Mantell's figures are available for the interpretation of the species. They are much stylized, the dimensions of the specimens are not recorded, and there is confusion as to the true locality of the material. *Crisia johnstoniana* Mantell was recorded by Mantell (1844, p. 285; 1854, p. 269) from the Lower Greensand of Maidstone, Kent, and possibly from the Shanklin Sands of the Isle of Wight. The systematic position of *Crisia johnstoniana* is quite uncertain, and we doubt whether it can be referred to *Rhammatopora*.

Stratigraphical distribution. Albion to Cenomanian, upper part of zone of *Schloenbachia varians*.

Key to the species of *Rhammatopora*

1. Aperture up to 0.45 mm. long and up to 0.25 mm. wide; number of apertural spine-bases 15–20 (commonly 18) 1. *R. gaultina* (Vine)
2. Aperture up to 0.27 mm. long and up to 0.17 mm. wide; number of apertural spine-bases apparently 10–13 (commonly 12) 2. *R. gasteri* sp. nov.

Rhammatopora gaultina (Vine)

Plate 62, figs. 1, 2

Membranipora gaultina Vine 1890, pp. 461, 484, pl. 19, fig. 13a–d; 1891a, pp. 385, 396; 1892, pp. 154, 155, pl. 6, fig. 15; 1893, p. 335.

Membranipora gaultina var. Vine 1891b, p. 395.

Rhammatopora gaultina (Vine); Lang 1915, pp. 498, 499, pl. 17, fig. 2.

Rhammatopora pembroekiae Lang 1915, pp. 498, 499, pl. 17, figs. 3, 4.

Rhammatopora vinei Lang 1915, p. 498, pl. 17, fig. 1.

Pyripora gaultina (Vine); Bassler, 1935, p. 189.

EXPLANATION OF PLATE 62

Figs. 1, 2. *Rhammatopora gaultina* (Vine). 1, Holotype of *Rhammatopora pembroekiae* Lang, D. 22987, uni- and bi-laterally budded normal zooecia with minute apertural spine-bases, $\times 20$. 2, Holotype of *Rhammatopora gaultina* (Vine), D. 2062, normal zooecia with minute apertural spine-bases, $\times 20$.

Figs. 3, 4. *Rhammatopora gasteri* sp. nov. Holotype, D. 40472. 3, Part of zoarium with normal zooecia with minute apertural spine-bases, $\times 35$. 4, Detail of two zooecia and part of a damaged third zooecium, the most distal zooecium with two very distinct spine-bases on the distal part of the apertural rim, $\times 75$. Photographs by Dept. of Photography, University of Durham, King's College, Newcastle upon Tyne.